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Contribution of dark septate fungi to the nutrient uptake and growth of rice plants

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ABSTRACT

The use of dark septate fungi (DSE) to promote plant growth can be beneficial to agriculture, and these organisms are important allies in the search for sustainable agriculture practices. This study investigates the contribution of DSE to the absorption of nutrients by rice plants and their ensuing growth. Four DSE isolates that were identified by ITS phylogeny were inoculated in rice seeds (Cv. Piauí). The resulting root colonization was estimated and the kinetic parameters V_{max} and K_m were calculated from the nitrate contents of the nutrient solution. The macronutrient levels in the shoots, and the NO_3^--N, NH_4^+-N, free amino-N and soluble sugars in the roots, sheathes and leaves were measured. The rice roots were significantly colonized by all of the fungi, but in particular, isolate A103 increased the fresh and dry biomass of the shoots and the number of tillers per plant, amino-N, and soluble sugars as well as the N, P, K, Mg and S contents in comparison with the control treatment. When inoculated with isolates A103 and A101, the plants presented lower K_m values, indicating affinity increases for NO_3^--N absorption. Therefore, the A103 *Pleosporales* fungus presented the highest potential for the promotion of rice plant growth, increasing the tillering and nutrients uptake, especially N (due to an enhanced affinity for N uptake) and P.

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Introduction

Despite the increasing yields caused by genetic progress over the last 30 years, improvements in crop yields have not been very evident, especially for rice,[1,2] which is the most frequently cultivated and consumed cereal in the world.[3] That said, farmers have to face the increased costs of seeds, chemicals, and fertilizers.[2] In this scenario, increasing crop yields at lower costs could be achieved by increasing the root surface provided by associations with fungi, culminating in better nutrient uptake and plant health.[4,5]

Dark septate fungi (DSE) are ascomycetes, and they are characterized by having dark pigmentation, microsclerotia and melanized septate hyphae that colonize the root epidermis and cortex inter- and intracellulary in the host roots.[6–11] Many of these fungi are able to colonize the root cells of plants, promoting growth without causing pathologies.[12,13]

These fungi often inhabit oligotrophic soils that are associated with the roots of hundreds of plant species in all climate regions and major biome types.[12,14–20] Although DSE research is increasing, our knowledge of the diversity of these fungi remains restricted.[21] DSE classification is gradually being improved and new species are being described, but many isolates do not yet have adequate taxonomic positioning.[21,22] For example, the three novel genera *Darksidea*, *Aquilomyces* and *Flavomyces* belonging to *Lentitheciaceae*, *Morosphaeriaceae* and, *Massarinaceae* family were recently documented.[21] To date, approximately 40 DSE species have been described.[6,21,23–26]

The ability of these fungi to promote plant growth has attracted attention because of their potential use in different species, such as conifers, grasses, and cabbages, among others.[6,22,27–29] Furthermore, because they readily grow in culture media and are not biotrophic, DSEs have advantages over other fungi because their inoculant production can be easier.[6,30] Newsham[13] performed a meta-analysis of 18 independent studies to assess the inoculation of DSE in different crops, concluding that this practice raised the nitrogen (N) and phosphorus (P) concentrations as well as the plant biomass by 26–103%. Conversely, another meta-analysis suggested negative to neutral effects from inoculating with non-clavicipitaceous root fungal endophytes (including DSE) on the plant biomass and N content.[31] Although the influence of DSE on its host is still under debate, the identification of DSE with biotechnological potential expands the horizons for its use in agriculture, as is also the case for nitrogen-fixing bacteria and other beneficial microorganisms.

In Brazil, recent studies have shown the presence of DSE in the roots of healthy *Oryza glumaepatula* plants in the natural environment.[32] In this study, some isolates were able to colonize and contribute to the development of *Oryza sativa* L. without causing disease symptoms.[32–34] In the same way, based on intergenic spaces, Bonfim et al.[35] identified 35 DSE groups representing 27 species that were isolated from 7 native trees, indicating the high diversity of these fungi. Likewise, a new dark septate fungus species from China (*Harpophora oryzae*) was recently identified in the healthy roots of *Oryza granulata*, which was able to increase the biomass of *O. sativa*, also without triggering disease symptoms.[22]

The way in which DSE establish their association with the host is not fully understood, but studies have indicated that growth promotion can be performed directly, by enhancing the nutrient uptake; or indirectly, by protecting the plant against abiotic stresses (drought, salinity, and high concentrations of heavy metals) and the production of phytohormones or analogous substances.[27,36–38] In *Brassica campestris* L., a mutualistic association was found with the fungus *Heteroconium chaetospira*, in which the fungus supplies N to the plant and the plant provides carbon to the fungus, resulting in significant increases in plant biomass.[27]

The best growth promotion responses from DSE use have been observed when organic sources of N are used.[12,13,27,28] However, because of the generalized occurrence of dark septate fungi in a wide range of environments,[20,39] there are likely DSE species that are also able to assist in nutrient uptake from inorganic sources.[27]

DSEs have been shown to form intraradical structures resembling those formed during mycorrhizal symbioses. For example, *Acephala macrosclerotiorum* formed ectomycorrhizae in pine and spruce[29] and *H. chaetospira* formed loose intracellular hyphal loops that morphologically resembled the ericoid mycorrhizae in *Rhododendron obtusum* var. *kaempferi*.[40] However, the roles of these intraradical hyphal structures are still at the hypothesis level.

In a previous study, the compositional diversity of the DSE that colonized native rice (*O. glumaepatula*) in the Brazilian Amazon was investigated.[33] Based on *in vitro* tests, 32 nonpathogenic isolates were considered as DSE fungi.[33] This study was performed to address the phylogenetic position and to assess the contribution of dark septate fungal isolates (A101, A103, A104 and A105) obtained from *O. glumaepatula*[33] to the absorption of nutrients and the growth of rice plants (*O. sativa*) under controlled conditions.

Materials and methods

Fungal isolates, DNA extraction, and phylogenetic analyses

All of the isolates investigated here are deposited in the COFMEA (Coleção de Fungos Micorrízicos Arbusculares da Embrapa Agrobiologia – https://www.embrapa.br/agrobiologia) (A101, A103, A104, and A105). For the phylogenetic analyses, genomic DNA was extracted from eight-day-old cultures grown in PDA medium. Five discs of 6 mm each were transferred from the plate to 2 mL sterile microtubes, to which 0.2 g of glass beads (106 μm; Sigma) and 1 mL of sterilized ultrapure water were added. The suspension was vigorously agitated by vortex and centrifuged (1.5 min; 13 000 rpm). The supernatant was transferred to clean microtubes, and 600 μL of the cell lysis solution from the kit Wizard® Genomic DNA Purification (Promega) was added. The samples were vigorously agitated by vortex (10 min) and subjected to three cycles of 95 °C/ice, with 10 min for each step. These cycles were followed by a Wizard® Genomic DNA Purification protocol. The

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